

THE ZOOGEOGRAPHY OF LESSER ANTILLEAN ANOLIS LIZARDS—AN ANALYSIS BASED UPON CHROMOSOMES AND LACTIC DEHYDROGENASES¹

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ABSTRACT

On each island bank of the Lesser Antilles, there are one or two distinct forms of iguanid lizards of the genus *Anolis*. On the basis of osteology, these anoles have been placed in two species groups, which show a sharp geographic break. The southern group (termed *roquet*) occupies all the islands from Grenada north to Martinique. The northern group (called *bimaculatus*) is found from Dominica, the island due north of Martinique, on through all the other Lesser Antillean islands. It also occurs on several of the Greater Antillean islands and island banks.

Differences in karyotype and in electrophoretic mobility of the protein lactic dehydrogenase amongst these Antillean lizards have permitted a detailed analysis of relationships, evolutionary history, and zoogeographic movement. The two species groups are distinct osteologically, chromosomally, and biochemically. The *roquet* group is characterized by 12 metacentric macrochromosomes, 22 or 24 microchromosomes,

and the absence of sex chromosomal heteromorphism. This karyotype appears to be primitive for the family Iguanidae and characterizes many genera, including a South American anoline genus. The lactic dehydrogenases of the *roquet* group are characterized by very slow anodal migration in borate buffer. The *bimaculatus* group is characterized by a reduced number of chromosomes, a less sharply marked break between macro- and microchromosomes, and male heteromorphism. Their lactic dehydrogenases migrate more rapidly towards the anode than do those of the *roquet* group.

Three subgroups of *bimaculatus* may be recognized; two are strictly Lesser Antillean and are characterized by 9 or 10 pairs of macrochromosomes, with no sharp break between the sixth and seventh pair. In the first of these, the *bimaculatus* group *sensu stricto*, all members have identical LDH mobilities. The second, *wattsi*, has only one species; in karyotype it is identical to most *bimaculatus*, but has a more rapidly migrating LDH. The third subgroup is found to the west of the Lesser Antilles on St. Croix, Puerto Rico, and Hispaniola. It is termed the *acutus* group. The LDH of *wattsi* is identical to that of two members of the *acutus* group. In chromosomes, the *acutus* group appears somewhat intermediate to the karyotypically primitive *roquet* group in the south, and its near-neighbor

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wattsi and *bimaculatus* groups. Like the *roquet* group, *acutus* has six pairs of meta-centric macrochromosomes, and the majority of the species have a sharp break between pairs six and seven. However, pair seven is not truly small enough to be called microchromosomal; it is intermediate in size. There is a sharp break between pair seven and the microchromosomes. Like the *bimaculatus* group, the *acutus* group is characterized by male chromosomal heteromorphism, and a male diploid number of 33 or less.

The karyotypes of some species of *Anolis* on Puerto Rico and Hispaniola are identical to that of the *roquet* group. It is argued that there were two colonizations of the Antilles from South America, one to the southern Lesser Antilles, ultimately giving rise to the *roquet* group; the second to the Greater Antilles. In the Greater Antilles, one stock arose that evolved a reduced diploid number and male heteromorphism. This group gave rise to the *bimaculatus* group, which became established in the northern Lesser Antilles. Furthermore, it is postulated that the *roquet* and *bimaculatus* groups were colonizing the Lesser Antilles at approximately the same time from opposite directions. The non-overlap between the two groups is due to competitive exclusion.

INTRODUCTION

On virtually every island in the Caribbean, there is at least one and sometimes as many as 25 species of small to moderate sized lizards of the genus *Anolis* (Fig. 1). This genus has always been difficult for systematists. In the preface to a series of papers on the anoles of the Lesser Antilles, Williams (1959: 188) wrote, "The segment of *Anolis* that is here reported on was believed to be, and may well be, the simplest areal segment of the genus in which more than one species occurs. . . . Yet we have found the complications formidable and not amenable to study on the basis of preserved specimens alone." Further, on the

same page Williams stated, "It is even more evident in this genus than in others that we cannot be prisoners of our conventional museum techniques, that a very wide approach will barely encompass the things we need to know." In this paper we escape from the "prison" of conventional museum techniques by entering the laboratory.

We chose to investigate biochemical and cytological characters because they provide an independent check on morphological characters and, quite simply, because they work. In a study of the relationships of the anoles of the southern portion of the Lesser Antilles (Gorman and Dessauer, 1966), we noted that lactic dehydrogenase (LDH) defined the *roquet* group: electrophoretic properties common to the LDHs of the *roquet* species group differed from those of all other anoles studied. Likewise, chromosome studies on *Anolis* (Gorman, 1965; Gorman and Atkins, 1966, 1967) indicated the value of karyotype as a systematic character. In our discussion of the northern Lesser Antillean anoles we shall rely primarily on these two characters. In tracing the biogeographic movements of the southern species group, we shall also utilize other information available to us.

GEOGRAPHY

The Lesser Antilles are the chain of Caribbean islands stretching from St. Croix south to Grenada. These are oceanic islands, never having been connected to the main continental land masses. On each of these numerous islands are found one or two native species of *Anolis*—a genus of lizard that has been outstandingly successful in colonizing the Caribbean. Some of the islands of the Lesser Antilles were once parts of larger islands only recently fragmented, and, as pointed out by Baskin and Williams (1966), "in treating the zoogeography of the Lesser Antilles, we must deal with the banks and not solely the present islands." As will be seen, each bank has at least one endemic form, and only one form has been



Figure 1. *Anolis roquet roquet* from Martinique. An adult male with throat fan extended in territorial display.

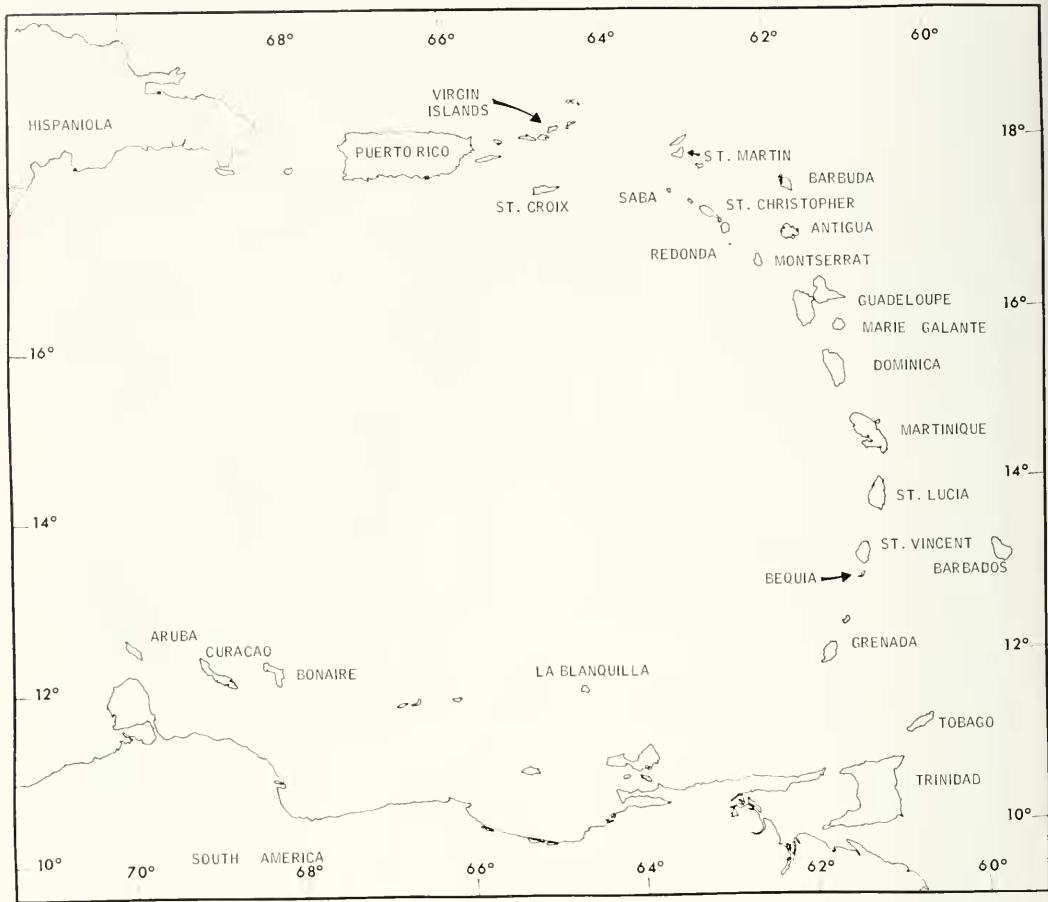


Figure 2. Map of the eastern Caribbean. The Lesser Antilles extend from St. Croix in the north to Grenada in the south.

successful in establishing itself on more than one island bank.

Two types of islands may be distinguished grossly in this archipelago: steep, montane, volcanic islands, which have high rainfall in at least some parts and are ringed either by steep cliffs or beaches of white or black sand; and low, flat, relatively xeric, limestone islands, ringed by white sand beaches only. These flat islands, presumably older, lie to the east of the montane islands and are sometimes called the outer chain. The southern limit of this outer chain is Marie Galante and the Grande Terre portion of Guadeloupe. It includes the Antigua bank and the Anguilla bank. Guade-

loupe itself is actually a double island; the western half is very mountainous. The mountainous chain begins in Grenada and continues north through Saba. Lying somewhat to the east of the main Lesser Antillean double chain is Barbados—also a relatively flat island with little topographic variation. Figure 2 shows the Lesser Antillean chain.

The *Anolis* on these islands fall into distinct species groups. Underwood (1959) called the group occupying the southern islands (from Grenada north to Martinique) the *roquet* group; those anoles on the northern islands were placed in the *bimaculatus* group. The groups were recog-

nized as distinct by Underwood, but the characters used to separate them were trivial, e.g., "in the *bimaculatus* group [the canthal ridge] is followed by a series of differentiated small supraciliaries; in the *roquet* group there is no differentiated series of small supraciliaries." And, "the caudal scales are arranged in whorls corresponding to the autotomy septa; in the *bimaculatus* group there are three or four dorsal crest scales in each whorl; in the *roquet* group there are usually five . . . if there are less it is only as an individual variation and not as a population character" (p. 193).

However, work by Etheridge (1960) and by Gorman and co-workers showed that the two major groups were quite distantly related. The *roquet* group was not recognized *per se* by Etheridge; all species within the group were placed in the *latifrons* series, a predominantly South American and presumably primitive series. Etheridge's concept of the *bimaculatus* group includes species in the northern Lesser Antilles, the Puerto Rico bank, Hispaniola, and the Bahamas. The two Lesser Antillean species groups differ profoundly in karvotype (Gorman and Atkins, 1967), display behavior (Gorman, 1968), and lactic dehydrogenase mobility in starch gel electrophoresis (Gorman and Dessauer, 1966). They are not closely related. That Underwood had to rely on trivial external characters to separate the groups emphasizes the fact that these two groups occupy virtually identical niches on islands of similar size and have thus been subject to similar selective pressures.

Our chromosome data are concordant with Etheridge's osteological data in that they indicate that the *roquet* group is primitive and the *bimaculatus* group more highly specialized (see Gorman, Atkins, and Holzinger, 1967; Gorman and Atkins, 1967).

Within the *bimaculatus* group in the Lesser Antilles, Underwood (*op. cit.*) singled out *wattsii* as being quite distinct in several characters, and he placed this species in a group of its own. We, too, shall

refer to the *wattsii* group. In addition, those members of the *bimaculatus* group *sensu* Etheridge that occur in the Greater Antilles and that were not considered by Underwood shall be called the *acutus* group. Etheridge's *bimaculatus* group will then consist of three elements: (1) the *bimaculatus* group *sensu stricto*; (2) the *wattsii* group; (3) the *acutus* group.

On Curaçao, to the west of Bonaire, and on the continental island of Trinidad are two species of a predominantly South American species group (*chrysolepis* group) that will not be reconsidered here (see Gorman and Atkins, 1967).

TAXONOMY

As Underwood wrote in 1959, "These lizards present the familiar nomenclatorial problem of island populations. Given a full knowledge of the relevant facts, which we certainly do not have, there remains a considerable element of personal taste in deciding how to represent them nomenclatorially." Since that time, the *roquet* species group has been intensively studied, and we are somewhat more confident about species relationships. Comparable studies have not been undertaken for the *bimaculatus* group. Underwood (1959) placed most of the island races as subspecies of *bimaculatus*. Lazell (1962 and 1964a) studied intra-island variation in the *bimaculatus* group of Dominica and Guadeloupe and named intra-island subspecies of *oculatus* and *marmoratus*, respectively. (The latter also has subspecies that occur on the islands satellite to Guadeloupe.) This report is not concerned with nomenclatorial designation. For the *bimaculatus* group we shall simply use the name of the form that is characteristic for a given island bank; we shall disregard Lazell's intra-island subspecific designations and shall not be concerned with whether Underwood considered the given form a subspecies of *bimaculatus* or a species. The *wattsii* group offers no problems—there is only one species and no named subspecies (*Anolis alter*, Williams,

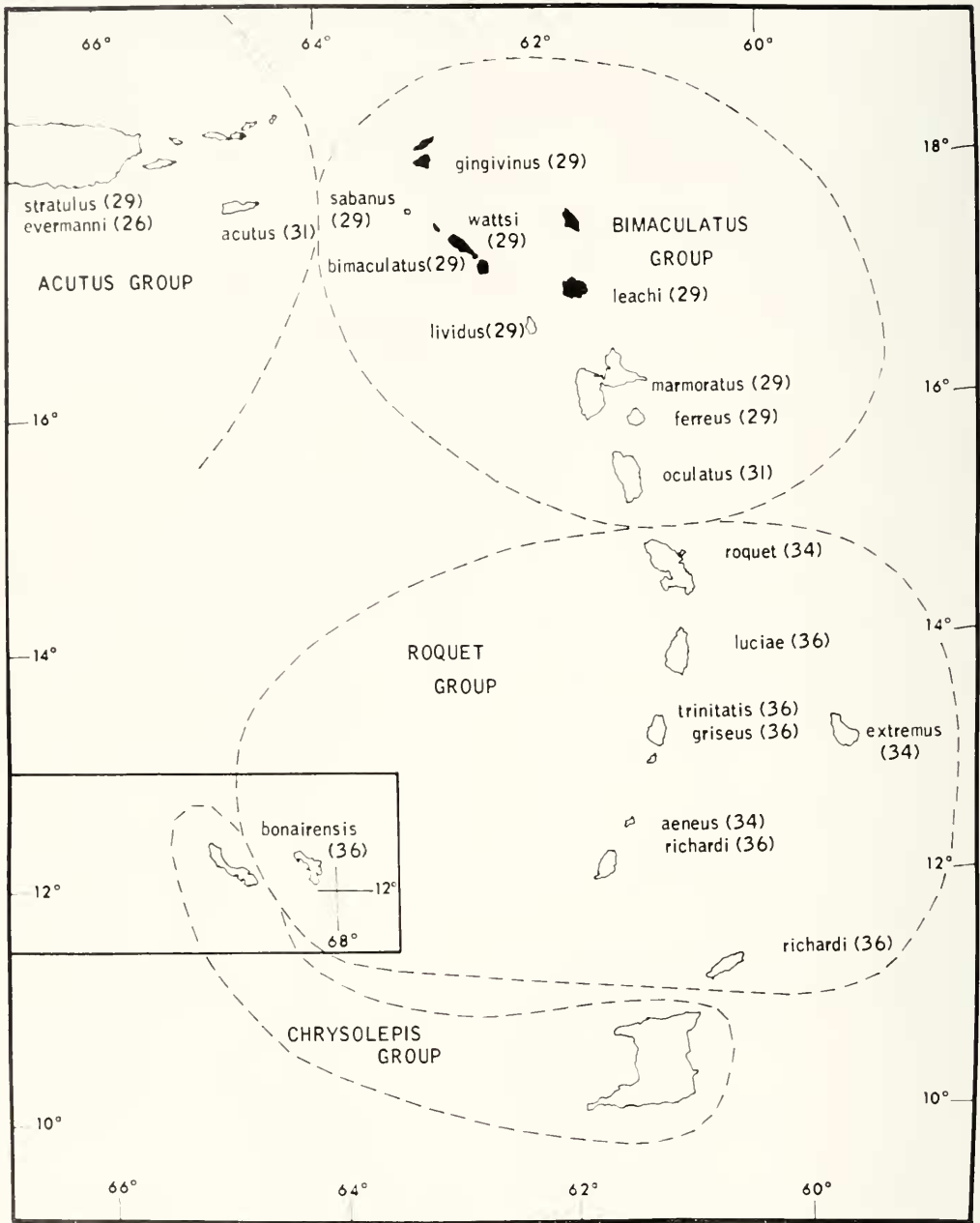


Figure 3. The distribution of Lesser Antillean *Anolis*. Species groups are separated by broken lines. The western part of the range is inset in solid lines. Numbers in parentheses are diploid chromosome counts for males. Names of forms are adjacent to the islands on which they occur. Only one species, *wattsi*, is found on more than one Lesser Antillean bank; its distribution is indicated by black islands. On each of these islands, *wattsi* is sympatric with a *bimaculatus* group form. In addition, *richardi* is found not only on the Grenada bank, but on Tobago, which geologically is not part of the Lesser Antilles. One member of the *acutus* group, *Anolis distichus* (2n = 33), is found on Hispaniola, the Bahamas, and Florida, north and west of the area included on the map.

1962, is a synonym of *wattsi*: Williams, personal communication). The *acutus* group also offers no problems, as the species are well defined. Names for the *roquet* group will follow Gorman and Dessauer (1966).

The distribution of these species groups and the forms considered are illustrated in Figure 3.

The important points illustrated by this figure are:

(1) There is complete exclusion between the *roquet* group and the *bimaculatus* group. (2) The break between the two groups falls between Martinique and Dominica. (3) There is nothing geologically "natural" about this break, i.e., it has nothing to do with the inner chain and outer chain. (4) Only one Lesser Antillean form, *wattsi*, has successfully colonized more than one island bank.

MATERIALS AND METHODS

Chromosomes were studied either by direct preparation of gonads for meiotic as well as mitotic cells, or by tissue culture of blood or lung, following Gorman and Atkins (1966).

To study LDH, crude extracts of hearts were made by grinding fresh or frozen tissue in a glass tissue grinder. Hearts from a population were from either a single animal or pooled samples. This made no difference, as we have found no intrapopulational variation in electrophoretic mobilities of heart LDH. The tissue was ground in a 0.25 M sucrose solution. No effort was made to maintain a constant tissue weight/volume of solution. Approximately 2 ml of sucrose were used per 0.05 grams of heart. The extracts were then compared by means of starch-gel electrophoresis, following the outlined procedure of Fine and Costello (1963).

Tissue LDH of anoles, as of many other animals, shows five distinct electrophoretic bands (Gorman and Dessauer, 1966). These result from the tetrameric association of hybrids of two distinct proteins termed heart (H) LDH and muscle (M) LDH.

Thus the five bands represent H_4 , H_3M , H_2M_2 , HM_3 , and M_4 (Salthe *et al.*, 1965). The two types H and M are so named because they predominate in those tissues. In this study all results are based upon differences in the mobilities of the H_4 LDH, which were more striking than differences found in the more slowly migrating M_4 LDH.

RESULTS

Roquet group

The chromosomes of the *roquet* group have already been discussed (Gorman and Atkins, 1967). Five forms, *luciae*, *trinitatis*, *bonairensis*, *griseus*, and *richardi*, have six pairs of metacentric macrochromosomes and twelve pairs of microchromosomes ($n=18$, $2n=36$). The other three forms, *aeneus*, *roquet*, and *extremus*, have a similar macrochromosomal complement, but only eleven pairs of microchromosomes ($n=17$, $2n=34$). There is no evidence of sex chromosomal heteromorphism.

The biochemical study on the *roquet* group (Gorman and Dessauer, 1966) indicated that the group was characterized by an anodally slow LDH. This work was based upon LDH in red blood cells, and resolution was not clear. Comparison of heart LDHs shows that seven forms have an electrophoretically identical LDH, while *richardi* (Grenada bank and Tobago) has an LDH of slightly faster anodal mobility (Fig. 4).

Bimaculatus group *sensu stricto*

The karyotype of the *bimaculatus* group differs considerably from that of the *roquet* group. It was in this species group that sex chromosomes in lizards were first demonstrated (Gorman and Atkins, 1966). Our original report showed that *bimaculatus*, *leachi*, *ferreus*, and *gingivinus* were all characterized by male $2n=29$, female $2n=30$. In meiosis of the male, there are 9 large bivalents decreasing gradually in size, 4 microbivalents, and a sex trivalent. In mito-

Figures 4 and 5. Heart lactic dehydrogenases of Lesser Antillean anoles. Drawings from starch gels. Each figure is a composite of several electrophoretic runs. Only samples on the same gel may be compared directly, as different gels were run for different lengths of time. All migration is anodal (toward the +). Site of sample application is marked by horizontal line below code letter. Small vertical bars separate individual gels.

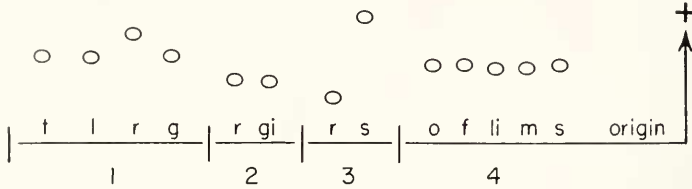


Figure 4. Gel 1. The roquet group. Phosphate buffer pH 7.0; t, *trinitatis*; l, *luciae*; r, *richardi*; g, *griseus*. All members of the group have identical LDH mobility except for *richardi*, which is slightly faster. Gel 2. Comparison of *richardi* (r), the "fastest" of the roquet group, with *gingivinus* (gi) of the *bimaculatus* group. Phosphate buffer pH 7.0. Migration rates approximately equal. Gel 3. Comparison of *richardi* (r) with *sabanus* (s) of the *bimaculatus* group. Borate buffer pH 8.6. In barate buffer the roquet group is characterized by very slow anodal migration. Gel 4. The *bimaculatus* group. Phosphate buffer pH 7.0. All members have identical LDH mobility. Shown here are *oculatus* (o), *fereus* (f), *lividus* (li), *marmoratus* (m), and *sabanus* (s).

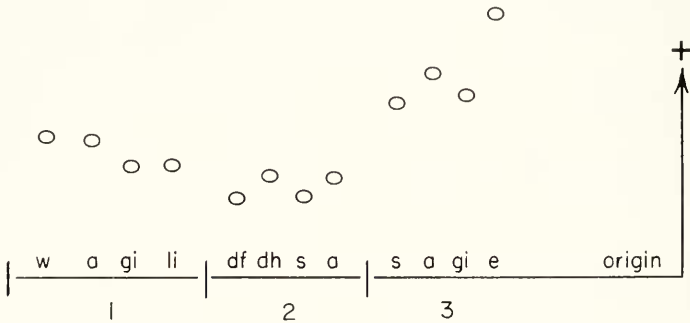


Figure 5. All phosphate buffer pH 7.0. Gel 1. Comparison of *wattsi* and *acutus* with *bimaculatus* group. Both *wattsi* (w) and *acutus* (a) have faster anodal migration than the members of the *bimaculatus* group (illustrated are *gingivinus* (gi) and *lividus* (li)). Gel 2. LDH variation in the *acutus* group. Interspecific variation in *distichus* from Florida (df) and Haiti (dh). The mobility of *stratulus* (s) falls between these two; *acutus* (a) appears identical to *distichus* from Haiti. Gel 3. Comparison of *acutus* and *bimaculatus* groups. The fastest LDH mobility is that of *evermanni* (e). The mobility of the *bimaculatus* group, represented by *gingivinus* (gi), is intermediate to that of *acutus* (a) and *stratulus* (s).

sis there are thus 13 pairs of chromosomes, and three unpaired chromosomes, an acrocentric X_1 , microchromosome X_2 , and a metacentric Y. Females are $X_1X_1X_2X_2$. Meiosis in females has not been studied. Further study of *sabanus*, *marmoratus*, and *lividus* shows these to be quite similar to those previously cited. Only one member of the *bimaculatus* group differs in karyotype: *A. oculatus* from Dominica, the southernmost island inhabited by this group. As already reported (Gorman and Atkins,

1967), *oculatus* has a similar sex chromosomal mechanism but a higher number of autosomes (male $2n=31$, female $2n=32$). The difference appears to be Robertsonian—one pair of small metacentric macrochromosomes present in all other members of the *bimaculatus* group is represented by two pairs of acrocentric chromosomes in *A. oculatus*. Figures 6A and B compare meiotic chromosomes in two members of the *bimaculatus* group, and Figures 7A and B compare mitotic karyotypes in two forms.



Figure 6. Diakinesis in males of the *bimaculatus*, *wattsi*, and *acutus* groups. A.—*oculatus* (*bimaculatus* group). There are 15 bodies, 14 bivalents and a sex trivalent on the far right. The thin thread connecting one element of the trivalent has been retouched with two dots of ink (republished with permission from Systematic Zoology). B.—*sabanus* (*bimaculatus* group). There are 13 bivalents, and a sex trivalent on the far right. C.—*wattsi* (*wattsi* group). Virtually identical to *sabanus*. D.—*acutus* (*acutus* group). There are 14 bivalents, and a sex trivalent on the far right. Giemsa stain in all chromosome preparations.

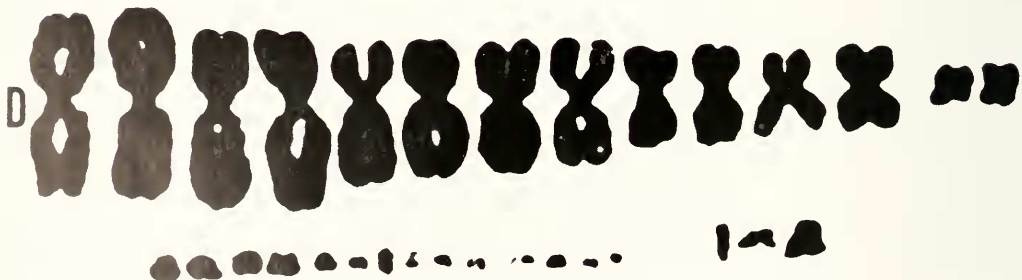
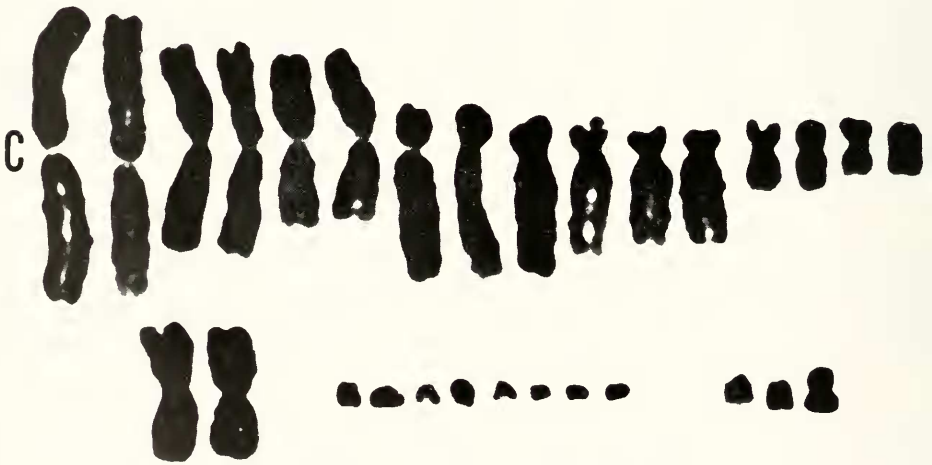
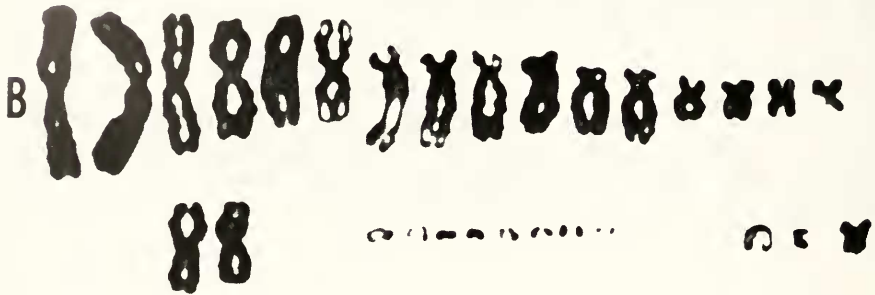
All members of the *bimaculatus* group have identical H LDH electrophoretic mobility. The LDH of *richardi*, the fastest migrating LDH in the *roquet* group, is approximately equal in mobility to that of the *bimaculatus* group in phosphate buffer gel (pH 7). However, in borate buffer (pH 8.6), the LDH of *richardi* and those of all members of the *roquet* group have relatively slow anodal mobility; the LDH band is well behind that of the *bimaculatus* group (Fig. 4).

Wattsi group

We have compared *wattsi* from St. Martin and Antigua and have found no differences in karyotype and LDH mobility. The karyotype of *wattsi* appears virtually identical with that of typical *bimaculatus* (Fig. 6C). In LDH, the mobility is slightly faster than in the *bimaculatus* group (Fig. 5).

Acutus group

The species of this group do not form a tight unit—neither in LDH nor in chromo-



somes—and each will be discussed separately.

A. acutus (St. Croix): The heart LDH mobility of this species appears identical with that of *wattsii* (Fig. 4). The karyotype however, differs from that of *wattsii* and of all other anoles previously described. In meiosis there are 14 autosomal bivalents and one sex trivalent, $2n=31$. While this number in itself is not different from that of *A. oculatus* of the *bimaculatus* group *sensu stricto*, the morphology of the chromosomes is quite different. There are six large pairs of metacentric macrochromosomes, and then a small seventh pair somewhat intermediate in size between the macro- and microchromosomes. There are eight pairs of microchromosomes, one of which must represent the X_1 and X_2 , and there is an unpaired small metacentric Y. Whether the X_1 and X_2 are heteromorphic, as is the case in typical *bimaculatus* anoles, could not be ascertained. No females were available for study. Figures 6D and 7D illustrate meiotic and mitotic chromosomes.

A. distichus: Lizards from Bimini, New Providence (Bahamas), Florida (introduced population), and Port-au-Prince, Haiti, were studied. There are 15 bivalents and a sex trivalent at meiosis (Fig. 9E); male $2n=33$, female $2n=34$. This a formula unique among the anoles studied by us to date (more than 70 species and subspecies). The macrochromosomal complement consists of seven pairs of metacentric or slightly submetacentric chromosomes. However, in this case, there is a sharp break in size between pairs 5 and 6, whereas in the other members of the *acutus* group and in the *roquet* group the break

comes between pairs 6 and 7. Both sexes have eight pairs of microchromosomes. The male has three unpaired sex chromosomes, a submetacentric Y and two heteromorphic acrocentrics (X_1 and X_2) (Fig. 7A); the female is $X_1X_1X_2X_2$.

In LDH there has been interpopulation differentiation. Hispaniolan *distichus* has a rapidly migrating H LDH that appears identical to those of *acutus* and *wattsii*, whereas specimens from Bimini and Florida populations have slower anodal mobility (Fig. 4).

A. stratulus (Puerto Rico): At meiosis there are 13 bivalents and one sex trivalent (Fig. 9D), male $2n=29$ (Fig. 8B). While this count is like typical *bimaculatus*, again the karyotype is quite unique. In mitotic metaphase there are six pairs of metacentric macrochromosomes and a sharp break between pairs six and seven; the seventh pair is also metacentric, being somewhat intermediate in size between the macrochromosomes and the six pairs of microchromosomes. In males there are three unpaired sex chromosomes. Females have not been available for study. In H LDH, the mobility is slower than in *acutus* and slightly faster than in Bahaman *distichus* (Fig. 5).

A. evermanni (Puerto Rico): This anole is most distinct both in karyotype and LDH mobility. It has the most rapidly migrating H LDH, the mobility being approximately 1.5 times faster than that of *acutus* (Fig. 5). In chromosomal formula it is also unique (Gorman and Atkins, 1968a). It is the only member of the *bimaculatus* group *sensu lato* that does not have the X_1X_2Y

Figure 7. Karyotypes in males of the *bimaculatus*, *wattsii*, and *acutus* groups. A.—*acutus* (*bimaculatus* group). $2n=31$. There are 28 autosomes and three unpaired sex chromosomes (shown on the far right of the second row). Leukocyte culture. B.—*fereus* (*bimaculatus* group). $2n=29$. There are 26 autosomes and three unpaired sex chromosomes (far right of second row). Note the marked similarity in the autosomes of *fereus* and *acutus* except that two pairs of acrocentric chromosomes of *acutus* (far left second row) correspond to one pair of metacentrics in *fereus*. Leukocyte culture (republished with permission from American Naturalist). C.—*wattsii* (*wattsii* group). $2n=29$. Virtually identical to *fereus* above. Direct testis preparation. D.—*acutus* (*acutus* group). $2n=31$. There are 28 autosomes and three unpaired sex chromosomes (shown on far right of second row). Leukocyte culture.

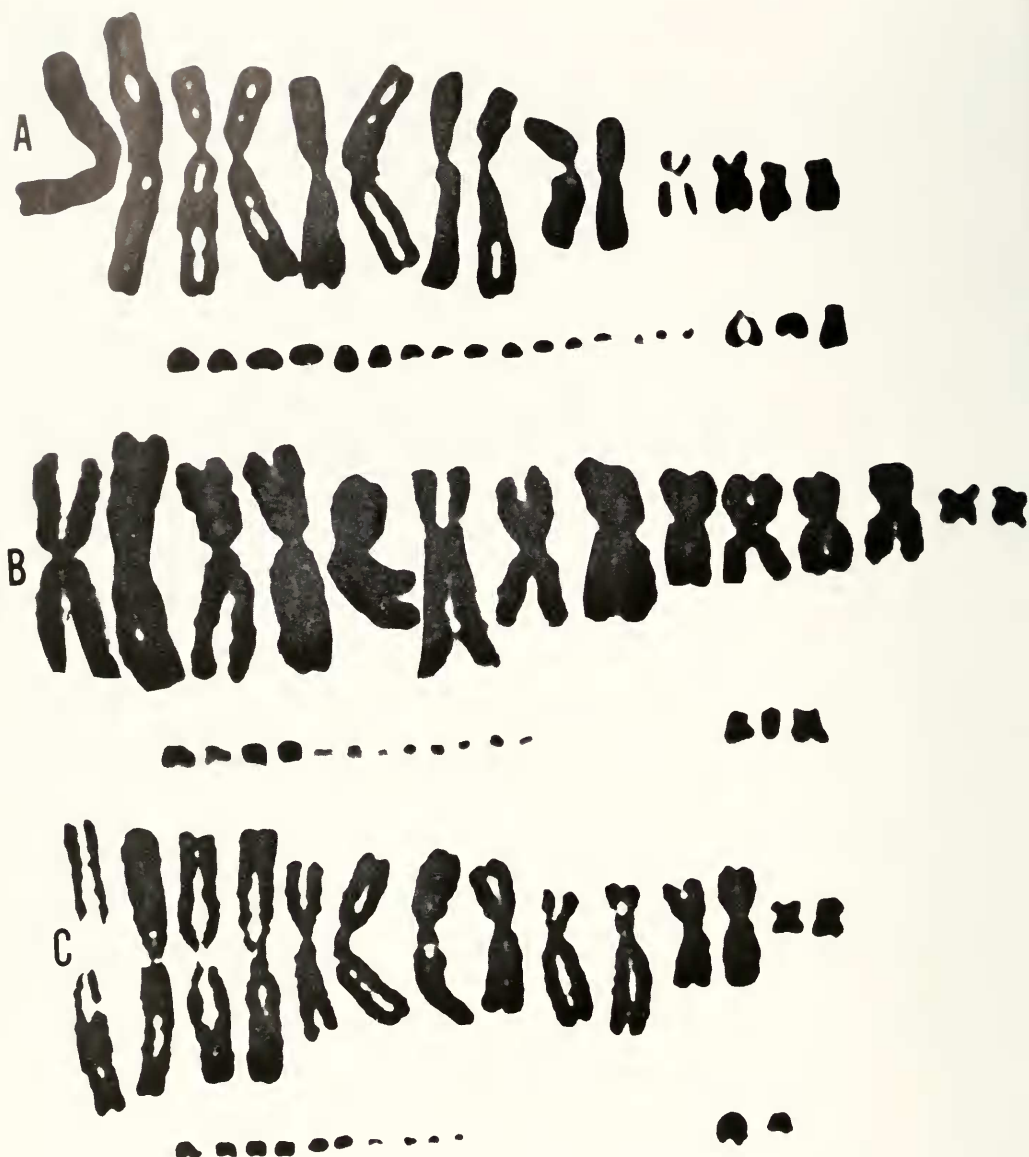


Figure 8. Karyotypes in males of the *acutus* group. A.—*distichus*. $2n = 33$. There are 30 autosomes and three unpaired sex chromosomes (shown on far right of second row). Leukocyte culture. B.—*stratulus*. $2n = 29$. There are 26 autosomes and three unpaired sex chromosomes (far right of second row). Direct testis preparation. C.—*evermanni*. $2n = 26$. This is the only member of the *bimaculatus* group with a heteromorphic pair of sex chromosomes (far right of second row). This is also the lowest diploid number reported in the genus *Anolis*.

sex chromosome system. Both males and females have diploid numbers of 26. However, in the male there is a heteromorphic pair of acrocentric chromosomes (Fig. 8C). As in *acutus* and *stratulus*, the six largest

macrochromosomes are meta- or submetacentric; there is a sharp break in size between pairs six and seven, and pair seven is also clearly metacentric. The sex chromosomes are the eighth pair.

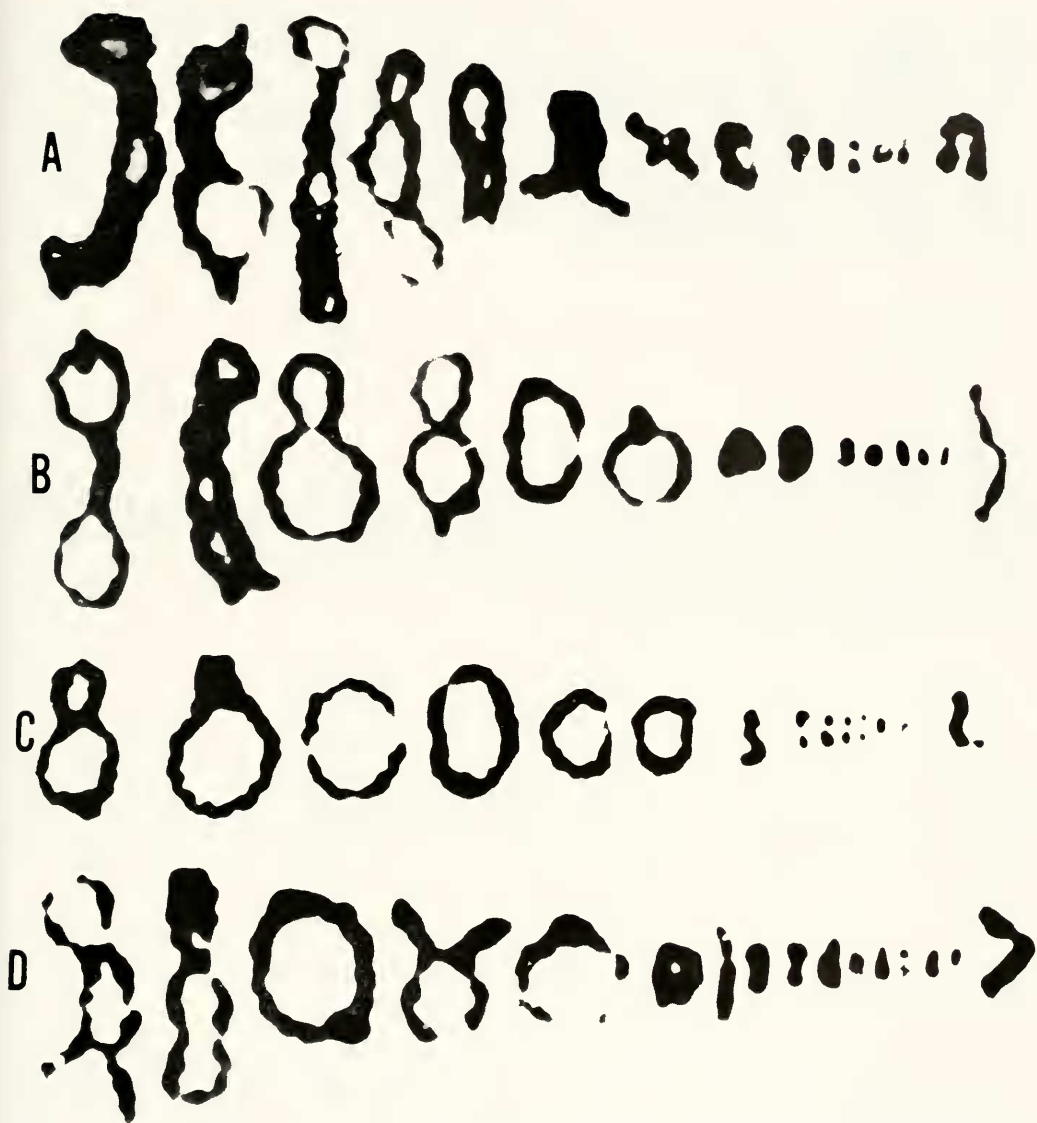


Figure 9. Diakinesis in males of the *crisatellus* and *acutus* groups. A.—*pulchellus*; B.—*gundlachi* (both *crisatellus* group). Each has six macro-, two intermediate, and five micro-bivalents; a sex trivalent is shown on the far right. C.—*stratulus* (*acutus* group). There are six macro-, one intermediate, and six micro-bivalents; a sex trivalent is shown on the far right. D.—*distichus* (*acutus* group). There are five macro-, two intermediate, and eight micro-bivalents; a sex trivalent is shown on the far right.

Chromosomal data on other Puerto Rican anoles

For comparative purposes, it is important to consider the information available on other Puerto Rican anoles. There are ten

species on the island. Two of these (*evermanni* and *stratulus*) belong to the *acutus* series and were discussed above. Six other species are placed by Etheridge in the *crisatellus* group, which he considers closely



Figure 10. Karyotypes of Puerto Rican *Anolis*. A.—*cuvieri* female. $2n = 36$. There are six pairs of metacentric macrochromosomes (top row), and 12 pairs of microchromosomes (second row). Males appear identical. There are no obvious heteromorphic sex chromosomes. Leukocyte culture. B.—*pulchellus* (*crstatellus* group) male. $2n = 29$. As in the above, there are six pairs of metacentric macrochromosomes. There is not a sharp break between macro- and microchromosomes. There are two intermediate sized pairs of metacentric chromosomes and five pairs of microchromosomes. There are three unpaired sex chromosomes (far right of second row). Two faintly stained microchromosomes were retouched with ink.

related to, and perhaps derived from, *bimaculatus*. The chromosomes of all the Puerto Rican members of the *crstatellus* group have now been studied. *A. cooki* and *A. crstatellus* were discussed in a recent paper (Gorman, Thomas, and Atkins, 1968). The diploid numbers for males are 29 and 27 respectively. Details will not be repeated here. The other four species¹ have karyotypes virtually identical to one another and quite similar to that of *A. cooki*. In meiosis there are six large bivalents, then a sharp break and two intermediate sized bivalents, five microbivalents, and an elongate sex trivalent. Figures 9A and B illustrate diakinesis in two forms (*gundlachi*

and *pulchellus*). The diploid number in males is 29 (Fig. 10B); we have not studied females.

The *crstatellus* group resembles several members of the *acutus* group in having six pairs of metacentric macrochromosomes with a sharp break in size between pairs six and seven, the smaller seventh pair also metacentric, and an X_1X_2Y sex chromosome system. The only difference, in fact, is that in the *crstatellus* group pair eight is also metacentric (compare Figs. 10B, 8A, B).

Only two other species of *Anolis* occur on Puerto Rico: one is a giant, *A. cuvieri*, the other a dwarf, *A. occultus*. Both are relatively poorly known; *occultus* was only discovered in 1962. Both species have the typical alpha *Anolis* chromosome comple-

¹ *A. gundlachi*, *A. krugi*, *A. poucensis*, *A. pulchellus*.

TABLE 1. THE FORMS STUDIED AND THE LOCALITIES FROM WHICH THEY WERE OBTAINED. THE LDH DATA ARE TABULATED INTO TWO MAJOR GROUPS, "RO" AND "BIM." THEY ARE DISTINGUISHED BY THEIR MIGRATION PATTERNS IN THE ALKALINE BORATE BUFFER, PH 8.6; "RO" IS CHARACTERIZED BY SLOW ANODAL MIGRATION; ALL "BIM" MIGRATE MORE RAPIDLY. RELATIVE RATES OF MIGRATION FOLLOW THE MAJOR GROUP CODE. HIGHER NUMBERS INDICATE MORE RAPID ANODAL MOBILITY IN STARCH GEL ELECTROPHORESIS.

Species group	Form	Island locality	Male diploid chromosome no.	LDH
<i>roquet</i>	<i>roquet</i>	Martinique	34	ro-1
"	<i>extremus</i>	Barbados	34	ro-1
"	<i>aeneus</i>	Grenada	34	ro-1
"	<i>luciae</i>	St. Lucia	36	ro-1
"	<i>bonairensis</i>	Bonaire	36	ro-1
"	<i>trinitatis</i>	St. Vincent	36	ro-1
"	<i>griseus</i>	St. Vincent	36	ro-1
"	<i>richardi</i>	Grenada	36	ro-2
<i>bimaculatus</i>	<i>lividus</i>	Montserrat	29	bim-3
"	<i>sabanus</i>	Saba	29	bim-3
"	<i>ferreus</i>	Marie Galante	29	bim-3
"	<i>marmoratus</i>	Guadeloupe	29	bim-3
"	<i>bimaculatus</i>	St. Christopher	29	bim-3
"	<i>leachi</i>	Antigua	29	bim-3
"	<i>gingivinus</i>	St. Martin	29	bim-3
"	<i>oculatus</i>	Dominica	31	bim-3
<i>wattsi</i>	<i>wattsi</i>	St. Martin and Antigua	29	bim-4
<i>acutus</i>	<i>acutus</i>	St. Croix	31	bim-4
"	<i>distichus</i>	Haiti	33	bim-4
"	<i>distichus</i>	Bahamas	33	bim-1
"	<i>stratulus</i>	Puerto Rico	29	bim-2
"	<i>evermanni</i>	Puerto Rico	26	bim-5
<i>cristatellus</i>	<i>cooki</i>	Puerto Rico	29	not studied
"	<i>pulchellus</i>	Puerto Rico	29	not studied
"	<i>poncensis</i>	Puerto Rico	29	not studied
"	<i>gundlachi</i>	Puerto Rico	29	not studied
"	<i>krugi</i>	Puerto Rico	29	not studied
"	<i>cristatellus</i>	Puerto Rico	27	not studied
Primitive alpha	<i>occultus</i>	Puerto Rico	36	not studied
"	<i>cuvieri</i>	Puerto Rico	36	not studied

ments. Study of mitosis in a female *cuvieri* revealed a karyotype of six pairs of metacentric macrochromosomes and twelve pairs of microchromosomes, $2n=36$ (Fig. 10A). We have seen only a few mitotic divisions in *A. occultus*; there are clearly twelve metacentric macrochromosomes, but the number of microchromosomes could not be determined accurately. However, in diakinesis there are clearly six large and twelve small bivalents.

Distributional and karyotypic data for the *wattsi*, *acutus*, and Puerto Rican species groups are illustrated on Figure 11. All data are summarized in Table 1.

DISCUSSION

General

Geologists have not provided us with much useful information about the age of the Lesser Antillean islands. In particular, some of the small islands may have had several cycles above and below the sea, but of this we can say little. Woodring (1954), in a general review, shows the Lesser Antilles of today to have been submarine volcanoes through the early Miocene (fig. 3, p. 728), but he makes no reference to when they appeared above the surface. In the region of the Greater Antillean islands of

Hispaniola and Puerto Rico there has been some land continuously since the Cretaceous.

How anoles colonize islands by over-water dispersal has never been observed, but it is not difficult to imagine. During the rainy season, and particularly following hurricanes, large mats of floating vegetation come north from the Orinoco, passing along the east coast of Trinidad. Occasionally, lizards and/or their eggs may take advantage of this transport system and journey into the sea. Most would perish. However, some of the rafts must come to rest on the beaches of the Lesser Antilles.

Reference to an Atlas of Surface Currents of the North Atlantic (Hydrographic Office, Washington, D. C.) shows a general northwesterly trend; but this is not absolute, and for short distances movement might be in any direction.

Although we lack useful fossils, precise dates for the age of the islands, and the exact direction in which currents moved potential colonists, we still feel that a careful analysis of the probable phylogenetic relationships of the island forms within their species groups provides a very likely hypothesis about the probable history of colonization routes. The value of such speculation has been stated by Wilson (1965): "Evolutionary hypotheses might never be definitive by the standards of experimental biology, but they are valuable if they are both falsifiable and heuristic. That is, to be valid they should make concrete predictions that are capable of being negated if the hypothesis is false; and they should point the way to deeper, more meaningful investigations if they are momentarily upheld."

The phylogenetic relationships of the two major species groups will be discussed independently. But first, it is worth stating, in some detail, rules for evaluating characters as indicators of phylogenetic relationship. We shall follow Hennig (1966), who presents a formalized, methodological approach. It is therefore necessary to define some of his terms.

Characters or character conditions from which transformation started in a monophyletic group are termed *plesiomorphous*, and the derived conditions *apomorphous*. The presence of plesiomorphous characters in different species is called *symplesiomorphy*, the presence of apomorphous characters *synapomorphy*—always with the assumption that the compared characters belong to the same transformation series. It follows that monophyly can be established only by synapomorphous characters.

It does not matter whether the synapomorphy (a') is present identically in all species, or whether it is present in different derived conditions (a' , a''). "Recognition that species or species groups with common apomorphous characters form a monophyletic group rests on the assumption that these characters were taken over from a stem species that only they share in common, and which already possessed these characters prior to first cleavage" (Hennig, 1966, p. 90).

If it is a question of determining the relationships *between* different species groups, "then it is of primary importance to show that each group has apomorphous characters, characters that are present only in it" (op. cit., p. 90).

Hennig feels that the concepts of symplesiomorphy and synapomorphy go beyond the range of what we ordinarily call homologous characters. "We started from the idea that a , a' , a'' are different characters in a transformation series. We can speak without reservation of homologous characters if a , a' , a'' are transformation stages of an organ. But the transformation a - a' - a'' may also consist in complete reduction of the organ. For example, the absence of the wings in fleas is undoubtedly an apomorphous character in comparison with the presence of wings in other holometabolic insects. On the other hand, the possession of wings is an apomorphous character in comparison to their absence in the so-called 'Apterygota.' In general we speak only of the homology of organs,

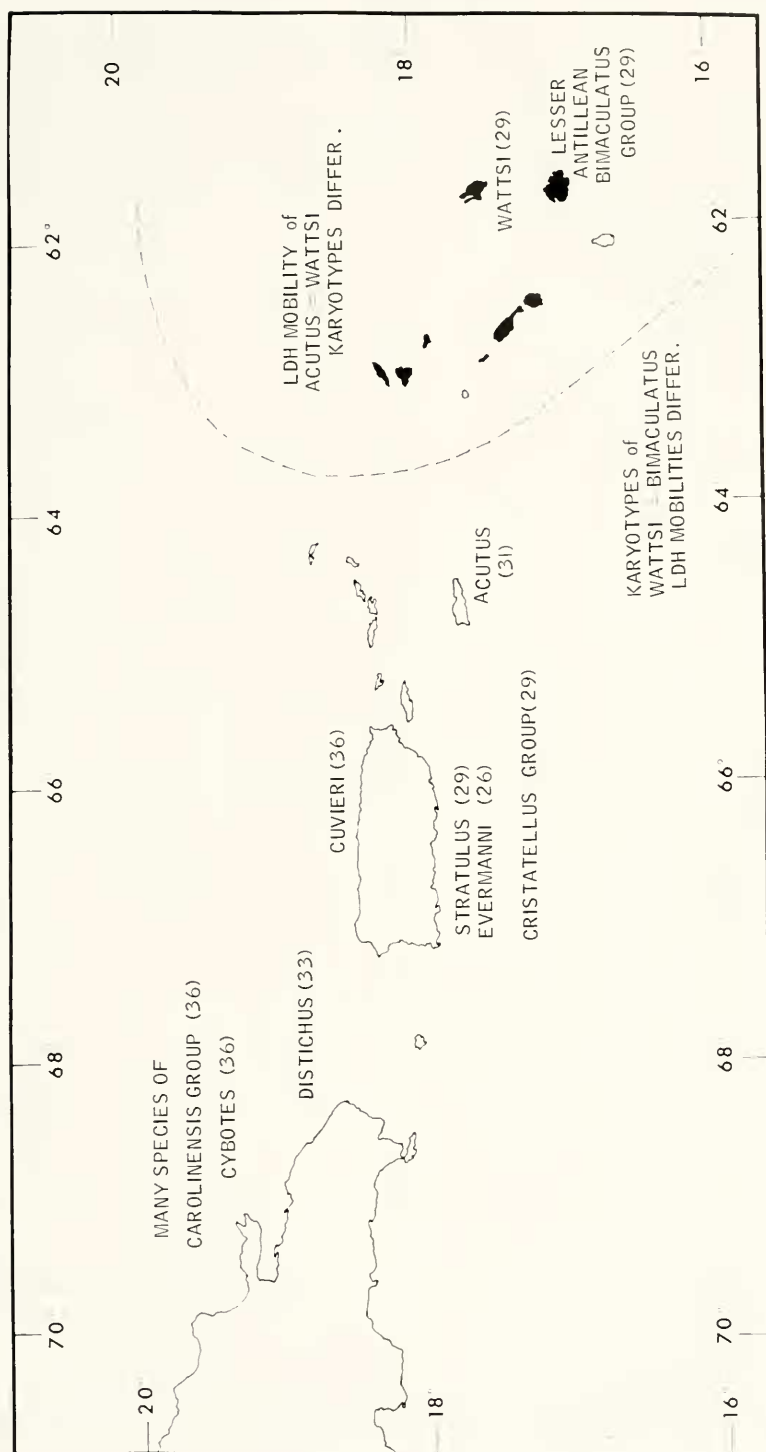


Figure 11. Distributional and karyotypic data for anoles of the *acutus*, *wattsi*, Puerto Rican, and Hispaniolan species groups. Numbers in parentheses are male diploid numbers. Islands shown in black are inhabited by *wattsi*. Dotted line separates the *wattsi* and *bimaculatus* group (to the east) from the *acutus* and Greater Antillean groups (to the west). A. *cybotes* of Hispaniola is considered a member of the predominantly Puerto Rican *cristatellus* group on the basis of osteology [Etheridge, 1960]. Chromosome data were presented in Gorman and Atkins (1966). Chromosome data for the western Caribbean *coralinensis* species group were presented in Gorman, Atkins, and Holzinger (1967).

but a 'character' may also be the absence of an organ."

The *roquet* species group

By all standard museum techniques, the eight forms in this group are extremely closely related. Etheridge (1960) did not mention any skeletal differences among the forms that comprise this group. In fact, the *roquet* group, along with one other species (*agassizi*), forms a subgroup within the *latifrons* series distinguished by the presence of functional autotomic caudal vertebrae (a presumably primitive character widespread in other lizards and secondarily lost in the mainland alpha anoles). Underwood (1959) did not discuss any major differences in scutellation among the members of the *roquet* group.

Does the group meet the test of monophyly using Hennig's criteria? The LDH is characterized by very slow electrophoretic mobility in alkaline buffer. This differs from every other *Anolis* so far studied, including *frenatus*, a mainland member of the *latifrons* series (Gorman and Dessauer, 1966). The territorial display of all members of the group is characterized by the dewlap being held extended for long periods of time, as opposed to the dewlap pumping of most other *Anolis*. It would appear that these behavioral and biochemical characters are synapomorphous and indicate monophyly.

The karyotype of $2n=36$ is common to many alpha *Anolis* and thus is plesiomorphous. Three members of the *roquet* group (*roquet*, *aeneus*, *extremus*) have the reduced chromosome number $2n=34$. This is the derived condition and most likely occurred only once.

Therefore, if we are to find one member of the species group that might be the most primitive, we will have to choose from the $2n=36$ group. Two of these five forms, *richardi* and *griseus*, are giant anoles. This appears to be a specialized condition that evolved under sympatry, under selective pressure for splitting the food niche.

Of the three remaining candidates (*luciae*, *bonairensis*, and *trinitatis*), *luciae* appears best to fill the requirements of a probable ancestor of the group. It is intermediate in size between the two giants and the other forms. St. Lucia, while not quite in the center of distribution of the species group, is somewhat centrally located—for there are *roquet* group members on islands to the southeast (Barbados), southwest (Bonaire), due north (Martinique), and due south (Grenada bank and St. Vincent).

Moreover, evidence from territorial display behavior supports the hypothesis of primitiveness for *luciae*. It will be recalled that members of the *roquet* group are characterized by not pumping the dewlap and that this appears to be the derived condition. In display, *luciae* bobs multiple series in a long head-bobbing sequence. As each series ends, there is a pause and an extremely slight dewlap retraction, then re-extension as a second series begins. This may well be a vestige of dewlap pumping (Gorman, 1968).

Is it likely that St. Lucia and not an island nearer to the South American mainland, such as Grenada or St. Vincent, would be first colonized? In point of fact, we know little about actual patterns of colonization of the islands. However, two genera of snakes, *Bothrops* and *Constrictor*, are known from St. Lucia and islands to the north, but not from St. Vincent or Grenada (Lazell, 1964b). It is possible that they have never reached the latter islands. The distance between St. Lucia and the nearest points on the mainland is not a great one for anoles to cross (approximately 200 miles); Williams (manuscript) has shown that *A. allisoni* has colonized the Islas de la Bahia from Cuba, travelling a distance of some 400 miles. Other iguanids have crossed from the South American mainland to the Galapagos, a distance of 600 miles.

If, in fact, the original colonists came on debris from the Orinoco, and they were swept slightly east out to sea as the currents

were moving north, the difference in distance from the mainland to Grenada or St. Lucia becomes negligible.

Let us accept for the moment the hypothesis that *luciae* is the most primitive member of the group and, in fact, that St. Lucia represents the ancestral home of the *roquet* group, and try to follow the sequence of colonizations (=phylogeny). We shall discuss possible alternatives later.

We infer that St. Vincent was twice colonized from St. Lucia; the second colonization took place after the first colonists had differentiated from the St. Lucia stock. There thus were two species on St. Vincent and, with two species sympatric, we might expect selection for size and habitat preference to reduce competition for food and to eliminate wastage of gametes in unsuccessful interspecific matings.

In fact, this model picture is precisely borne out by the anoles on St. Vincent. We find there *griseus*, a giant anole found primarily high in trees in deep shade, and *trinitatis*, a smaller species (and smaller than *luciae*) that occupies more open sites. Both retain the ancestral karyotype and LDH. In display behavior, *griseus* remains extremely close to *luciae*; the display of *trinitatis* is somewhat more modified.

The consistent color difference between the two species (*trinitatis* is green and unmottled; *griseus* is grey-brown and patterned) may have been fixed by selection as another recognition signal, in addition to size and habitat differences.

Next, we postulate that the giant *griseus* reached the Grenada bank, where it evolved into *richardi*. These two forms are very closely related on externals and, in fact, we know of no diagnosis that will separate them unequivocally. They were considered conspecific on the basis of blood proteins, which were very similar, including a common hemoglobin. The only difference found was in transferrin, a protein that appears to be evolutionarily labile in the Reptilia (Gorman and Dessauer, 1966). Now, however, we have found an LDH difference. Because

richardi's LDH differs from that of the other seven members of the species group, and since *richardi* is also a specialized form (giant) with a display less like that of *luciae* than is the display of *griseus*, it is logical to consider the LDH of *richardi* the derived (apomorphic) condition. The *richardi* of Tobago hardly differs from that of the Grenada bank, and recent colonization of this continental island from the Grenada bank is assumed.

The derivation of *A. bonairensis* is not clear. But it is possible that it, too, is derived from *A. luciae*. Bonaire lies far to the west of the main Lesser Antillean chain. However, *A. bonairensis* is certainly a member of the *roquet* species group, sharing common osteological (Etheridge, 1960), behavioral (Gorman, 1968), biochemical (Gorman and Dessauer, 1966), and cytological (Gorman and Atkins, 1967) characters. It is clearly within the species group in terms of blood proteins, but we could not place it particularly close to any one form. When the species was described (Ruthven, 1923), it was compared with *roquet* and *aeneus*. However, in chromosomes it falls within the primitive group and could hardly have been derived from *aeneus*. In display behavior it has unique species-specific components which seem, however, to be most similar to those of *luciae*.

Hummelinck (1940) described a subspecies of *bonairensis* called *blanquillanus* from the island of La Blanquilla (see Fig. 2), which lies approximately halfway between Grenada and Bonaire. Unfortunately, live lizards of this form have been unavailable for study. It is probable that *blanquillanus* is the living intermediate between *luciae* and *bonairensis*.

J. D. Lazell, Jr., who is studying the external morphology of Lesser Antillean anoles, informs us (personal communication) that in several characters *bonairensis* is most closely allied with *luciae*.

What then of the three forms with the reduced chromosome number? These three,

aeneus, *extremus*, and *roquet*, are very closely related, *inter se*, and have at times been considered conspecific (Underwood, 1959). Gorman and Dessauer (1965) showed that in terms of transferrins and hemoglobins the three form a linear series with *extremus* in the center. That is, *extremus* shares a common hemoglobin with *roquet*, and a common transferrin pattern with *aeneus*, while *roquet* and *aeneus* differ from each other in both these proteins.

The probable ancestor of this subgroup is *A. trinitatis*. On the basis of externals (other than color) it is only with great difficulty that one can distinguish *trinitatis* from *aeneus*. However, *trinitatis* differs from the subgroup in hemoglobin and transferrin (Gorman and Dessauer, 1966), display (Gorman, 1968), and by a pair of microchromosomes (Gorman and Atkins, 1967). The karyotypic difference, we now know, is even more profound. Studies of meiosis in *trinitatis-aeneus* hybrid males (Gorman and Atkins, 1968b) show an arrest at metaphase I, with poor pairing ability of the macrochromosomes; i.e., there are numerous univalents.

Colonization may have gone in one of two likely ways. Either from St. Vincent to Grenada, where chromosome loss occurred leading to *aeneus* (this loss of a chromosome pair could be interpreted as having been selected for as an additional isolating mechanism between the giant and the small species); or from St. Vincent to Barbados where chromosome loss was accidental but became established. If the former were the case, then the route of colonization would have been Grenada to Barbados to Martinique, whereas if Barbados were first colonized, there would have been a colonization in two directions, to Grenada and Martinique. It is fruitless to argue this further with our present state of knowledge.

Figures 12 and 13 summarize the possible colonization routes taken by the *roquet* group, as outlined above. A very important point in this hypothesis, and one that we shall return to later, is that Martinique was

the most recently colonized in the main chain.

The hypothesis of zoogeographic movements in this species group is based entirely upon the analysis of the phylogeny of the group. This produces a complex pattern of distribution. However, no simple model will suffice. Darlington (1957, p. 485) proposes two models to explain island patterns of distribution. One is termed the *immigrant pattern*. "Distance is basically important. Unless other factors are very unequal, animals dispersing from a continent to an archipelago may usually be expected to reach nearest islands first and to spread to other islands across the narrowest water gaps. The resulting pattern of distribution *should be orderly* [*italics ours*], with related forms occurring in series on adjacent islands along the route of immigration." This model is clearly not directly applicable to our system. For we would then expect that the island nearest the mainland (Grenada) would have anoles closest to the mainland stock—but, in fact, the two Grenada bank forms, *aeneus* and *richardi*, both have important apomorphous characters: *richardi* the derived LDH, and *aeneus* the derived karyotype.

Darlington's second model, to explain the *relict pattern*, is not at all applicable to the *roquet* group. "If a group of animals were once well represented on an archipelago and were then reduced in numbers and eliminated on some of the islands. . . the survivors would probably not form an orderly series on adjacent islands but would occur irregularly" (op. cit. p. 485). There is absolutely no evidence that leads us to believe that any anoles are relicts in the Lesser Antilles.

However, the model of movements that we propose does not really differ too much from Darlington's immigrant pattern, *if St. Lucia and not Grenada was the first colonized island*. Then, most subsequent colonizations are hops to the nearest adjacent islands; from St. Lucia to St. Vincent twice, from St. Vincent to the Grenada bank twice,

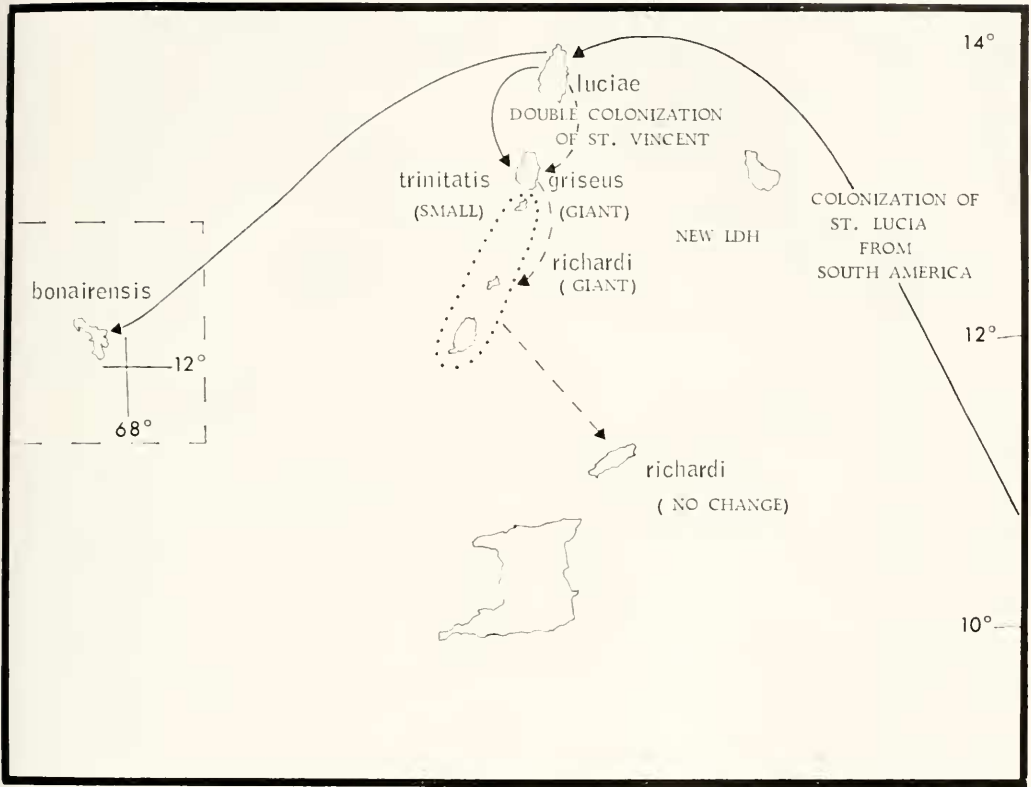


Figure 12. Possible colonization routes of the *roquet* group. Colonization of St. Lucia from South America and radiation from St. Lucia of the five forms with the primitive karyotype $2n = 36$. Broken arrows trace the path of the giant forms, solid arrows the small forms.

from the Grenada bank to Barbados, and from Barbados to the nearest available "empty" island, Martinique. Let us re-emphasize that the differences in distance from the Orinoco to St. Lucia and to Grenada are actually fairly negligible compared with the over-water colonizing ability already established for *Anolis*.

Furthermore, any hypothesis involving replacement or successive waves of colonization requires several long-distance over-water successful journeys. Yet, as Darlington states, "the death rate of most terrestrial animals during dispersal across salt water is presumably high and presumably forms a geometric progression: if only one individual in a thousand survives the crossing of a hundred miles of sea, only one in a

thousand of the remainder will be expected to survive the second hundred miles" (op. cit., p. 485). We would argue that the probability of successful colonization between adjacent island banks is much greater than the probability of multiple colonizations from the mainland, even though the proposed inter-island colonization may go against prevailing currents. Recall that over short distances, current movement may be in any direction.

There is a further factor that argues against multiple mainland colonization. Members of the *roquet* group are extremely closely related *inter se*; yet they are not very close to any living mainland forms. We would have to postulate extinction of an ancestor that was doing rather well and

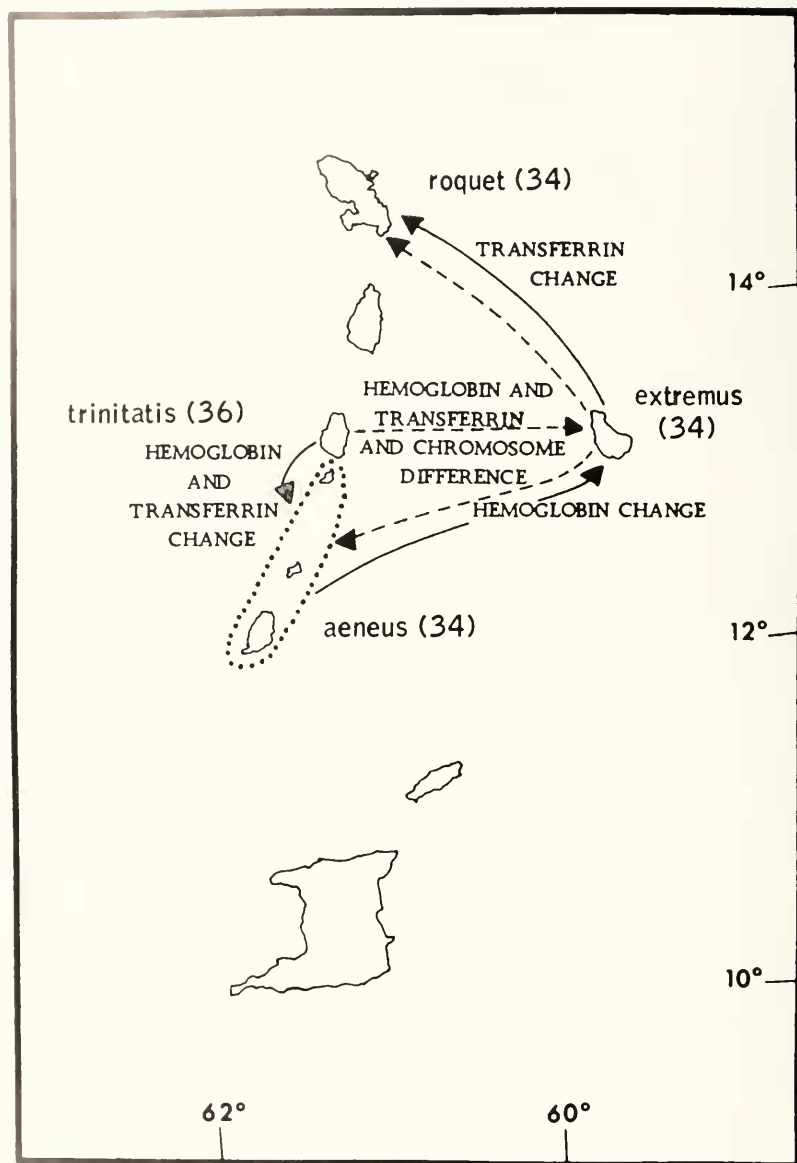


Figure 13. Possible colonization routes of the *raquet* group; the origin and dispersal routes of the advanced $2n = 34$ subgroup. Two possible pathways are illustrated. Both originate from St. Vincent where *trinitatis* $2n = 36$. Solid arrows show colonization to the Grenada bank, then to Barbados and then Martinique. Broken arrows show colonization from St. Vincent to Barbados and double colonization from Barbados to Grenada and Martinique.

sending out numerous colonists. There is no obvious reason why *roquet* group anoles would not do well on the mainland and, in fact, *aeneus*, which has been introduced

onto Trinidad and Guayana (present patterns of distribution could only be accounted for by introduction), is flourishing and possibly spreading. The simplest

model, then, is to consider the *roquet* group autochthonous to the Lesser Antilles.

The most difficult part of the *roquet* distribution to understand is the presence of *bonairensis* far to the west. To derive this species from *luciae* we must invoke long distance migration to the south (against prevailing currents) and west (with prevailing currents). An alternative might be via Blanquilla, and colonization of Blanquilla may have been from St. Vincent or, possibly, from Grenada *before* the establishment of chromosome loss in what ultimately became *aeneus* (see Fig. 12).

The *bimaculatus* species group

To understand the broad features of the Lesser Antillean *bimaculatus* forms, we must first examine the Puerto Rican situation. There, two species (*cuvieri* and *occultus*) have the primitive alpha anole karyotype characterized by six pairs of metacentric macrochromosomes, a sharp break between macro- and microchromosomes, and no obvious sex chromosomal heteromorphism. This appears quite unrelated to the karyotype of the *bimaculatus* group *sensu stricto*, which has complex sex chromosomal heteromorphism, an increased number of autosomal macrochromosomes, some of which are acrocentric or subacrocentric, and a correspondingly reduced break between the size of the smallest macrochromosomes and the microchromosomes.

While we do not have enough living intermediates to trace every part of the origin of the Lesser Antillean *bimaculatus* karyotype, the *acutus* group provides valuable clues. All members of this group have karyotypes that in some way resemble typical alpha *Anolis* (primitive) and Lesser Antillean *bimaculatus* (highly derived). In three species, *acutus*, *stratulus*, and *evermanni*, the six largest pairs of chromosomes are metacentric, and there tends to be a fairly sharp break between pairs six and seven, as in most alpha *Anolis*. But all members of the *acutus* group have diploid numbers reduced

from the primitive 36, and all but *evermanni* have an X_1X_2Y sex chromosomal mechanism. In these respects they resemble the Lesser Antillean *bimaculatus* forms.

Anolis distichus is unusual in the *acutus* series because the sharp break in chromosomes occurs between pairs five and six, instead of between six and seven. This is probably a derived condition resulting from additional translocations and rearrangements following the establishment of the *acutus*-like karyotype.

There is a similarity between the chromosomes of the *acutus* group and the beta anoles (see Gorman and Atkins, 1966, for figures). This is interpreted as convergence in the evolution of the karyotype. In both groups there is an increase in the number of metacentric macrochromosomes, seemingly at the expense of the microchromosomes.

What appears likely, then, is rapid evolution of the anole fauna on the Puerto Rico bank from a primitive alpha stock. This led to a group characterized by a reduced diploid number and a sex trivalent. Two groups emerged from this line, the *cristatellus* group and the *acutus* group. The two are karyotypically very similar, and on the basis of chromosomes alone, we would not have separated them. The most divergent member of the *acutus* group is *evermanni*, with its low chromosome number (the lowest known in the genus), rapid LDH mobility, and a heteromorphic pair of sex chromosomes rather than the three sex chromosomes. The *evermanni* stock probably diverged early and secondarily lost the X_1X_2Y sex chromosomal system.

It is significant that the LDHs of *wattsii*, *acutus*, and Hispaniolan *distichus* appear identical¹ whereas in chromosomes, *wattsii* and the Lesser Antillean *bimaculatus* group are similar. *A. wattsii* has traditionally been considered taxonomically close to *acutus* (e.g. Underwood, 1962: 70), and the LDH

¹ Identical electrophoretic mobility is suggestive of, but does not prove, structural identity of proteins.

finding corroborates morphological studies. The stock directly ancestral to *distichus* and *acutus* probably later underwent additional centric fusions and inversions leading to the *wattsi* karyotype; this stock in turn gave rise to the Lesser Antillean *bimaculatus* group, which evolved a new LDH that has remained constant in all races of the species group. These facts argue again for a single successful colonist in the northern Lesser Antilles which, through more or less stepwise colonization, filled the northern half of this chain, much as the *roquet* group in the south evolved by stepwise colonization, radiating from St. Lucia.

The similarity in LDH mobility of Hispaniolan *distichus* and *acutus*, the two species in the *acutus* group with the highest chromosome number, implies that this LDH may be primitive for the *acutus* subgroup. The peripheral Bahaman populations would have an apomorphous LDH, as would the Puerto Rican species *stratulus* and *evermanni*.

The four members of the *acutus* group have four distinct karyotypes and at least four different LDHs (there being interisland variation in *distichus*). The peripherally evolved Lesser Antillean *bimaculatus* group, although representing eight distinct forms (a ninth, *A. nubilus* from Redonda, was unavailable for study), has only one LDH and only two karyotypes. Note that in the *roquet* group, in which eight distinct forms were also studied, there are only two different LDHs and two different karyotypes. This may represent a canalization of certain characters in peripherally isolated populations when compared with the species-rich source area.

Because detailed behavioral and biochemical studies have not been undertaken for the Lesser Antillean *bimaculatus* group, we are unable to provide directional arrows based on the sort of evidence used for the *roquet* group. However, it appears clear that the primitive members of the group are in the northern and western parts of the range. In chromosomal characters, the

acutus group is intermediate between primitive alpha and *wattsi*. *A. wattsi*, in turn, shares an important character with *acutus* (LDH) and with Lesser Antillean *bimaculatus* (chromosomes). Thus the most highly derived forms, the *bimaculatus* group *sensu stricto*, are found at the extreme south and east of the range of the group.

If we assume that the colonization followed the simple immigrant pattern of Darlington, we would expect that the most primitive members of the series would be in the northwest (they are) and that colonization occurred in an almost stepwise manner south and east along the chain. Because this is against major currents, we would not expect any long distance "leap-frogging." But again, distances between islands are so small that short hops south could certainly occur. Thus it is not improbable that Dominica, the southernmost of the *bimaculatus* islands, was the last colonized, much as Martinique, the northernmost of the *roquet* islands, was probably the last colonized by that group.

This raises a discussion of karyotypic comparison of Dominica *oculatus* with other members of the *bimaculatus* group. Earlier, it was pointed out that the difference in karyotype was Robertsonian. The number of chromosomal arms is the same in *oculatus* and in the other members of the species group (see Figs. 7A, B). However, two pairs of acrocentric chromosomes in *oculatus* are represented by a single pair of metacentric chromosomes in all the other members of the species group.

Was there an increase in chromosome number by centric fission? The answer is probably yes. Centric fusions (reducing the diploid number) appear to be much more common than the reverse process (White, 1963), and centric fusion, or complete loss, is the mechanism that we postulate in the *roquet* group, in which three forms have the reduced chromosome number. Centric fission, however, has been substantiated in the Iguanidae (*Plica plica*, see Gorman, Atkins, and Holzinger, 1967). Why

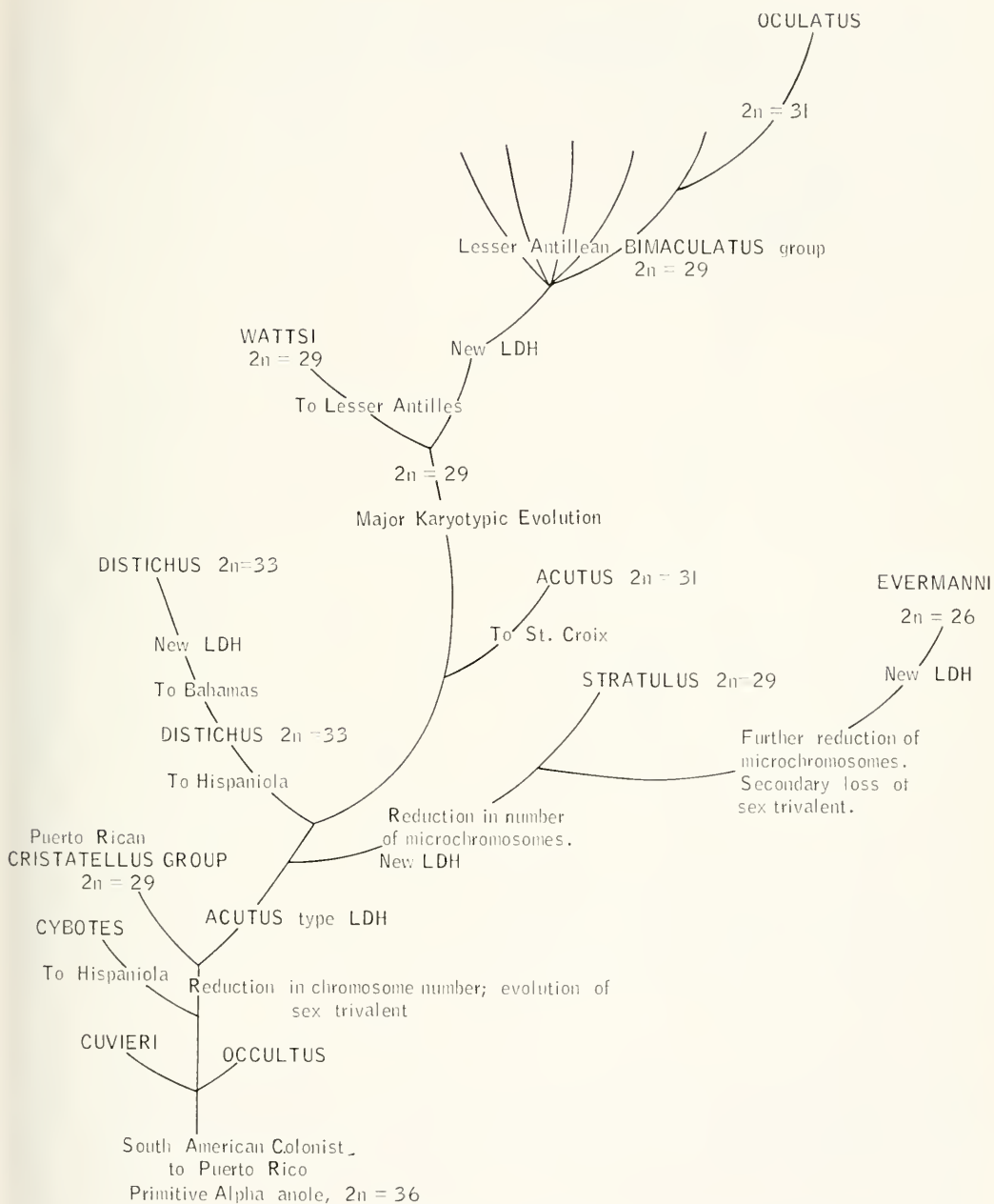


Figure 14. Proposed phylogeny of the *bimaculatus*, *acutus*, and Puerto Rican species groups of *Anolis*. Major changes in karyotype, LDH, and geographic movements are indicated.

is it invoked in this case? Aerocentric autosomes are unknown in any other alpha *Anolis*. The karyotype thus appears one

step more derived than the karyotypes of the other Lesser Antillean members of the *bimaculatus* series.

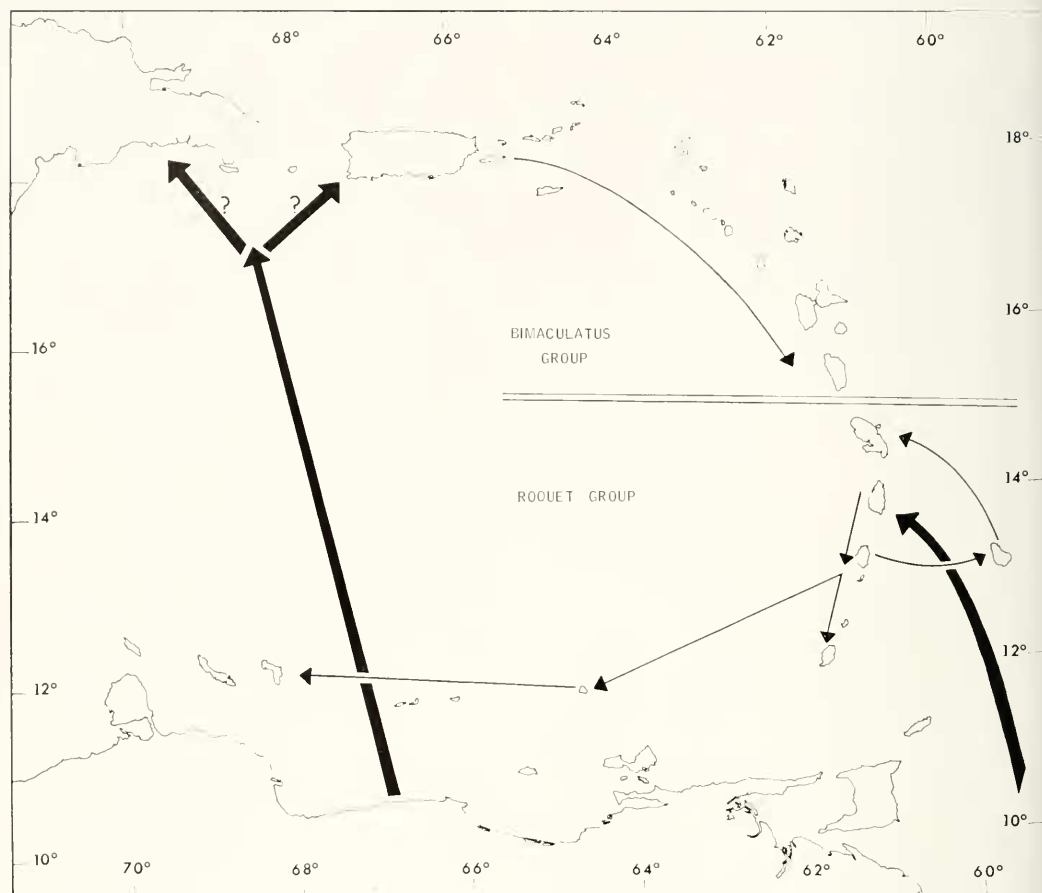


Figure 15. Summary of the general patterns of biogeographic movements. Heavy arrows indicate colonization from South America (they are not meant to imply exact paths). Two major movements are postulated. One is to the Greater Antilles, with subsequent colonization of the northern Lesser Antilles. This gave rise to the *bimaculatus* group. The second is to the southern Lesser Antilles, where the *roquet* group evolved. Light arrows indicate general movements within the species groups, as discussed in the text. The double horizontal line indicates the geographic break between the two Lesser Antillean species groups.

Utilizing the data from chromosomes and LDH, we can propose a model of the probable phylogenetic history of the Puerto Rican and northern Lesser Antillean anoles (Fig. 14).

There is only one inconsistency between this model and Etheridge's classification of anoles. Puerto Rican members of the *cristatellus* group have a derived karyotype. The common Hispaniolan species *A. cybotes* has the primitive alpha karyotype ($2n=36$) with the absence of sex chromo-

somal heteromorphism (Gorman and Atkins, 1966). Yet Etheridge (1960) places this species in the *cristatellus* group on the basis of osteology. It shares with the other members of this group not only the same osteological formulas (such as number of attached and free parasternals), but also an osteological character almost unique to the group—"jaw sculpturing" (one or more deep semilunar excavations on the lower surface of the dentary in adult males). If we are to reconcile this conflict, we could assume

that a proto-*cristatellus* stock colonized Hispaniola from Puerto Rico before the commencement of the reconstruction of the karyotype. Perhaps this stock had a tendency to evolve "jaw sculpturing," and the character arose in parallel in the two island populations. Or possibly, the character is convergent: there is one non-*cristatellus* group member (*A. argillaceus* of the *angusticeps* series) that has independently arrived at a similar condition (Etheridge, 1960, p. 74).

One final point needs discussion—the mutual geographic exclusion of the two Lesser Antillean species groups. Underwood (1959) wrote, "There is every reason to believe that anoles disperse readily; I am therefore at a loss to explain why the two groups do not overlap." It is clear, however, that one or two species of *Anolis* can easily saturate a Lesser Antillean island. The short distances between the islands must make it possible for waifs to cross from time to time. Yet each island bank has distinct forms. Once an empty island receives successful colonists, it probably takes a relatively short time for a nearly complete occupation of the generalized anole niche. Thus a new arrival to an island already colonized will suffer from the competition of numerous healthy, well-adapted congeners. The probability of successful establishment is thus much less than on a comparable island devoid of anoles.

In all cases in the Lesser Antilles where two species of anoles are sympatric, they differ greatly in size (*wattsii* is very small and is sympatric with several members of the *bimaculatus* group, including the two largest forms; *richardi* and *griseus* are very large and are sympatric with the two smallest *roquet* group anoles). There are also differences in habitat preference (Schoener and Gorman, 1968).

The Lesser Antilles were probably colonized at more or less the same time from two separate directions. The *roquet* group, derived from South America, filled the southern islands, while *bimaculatus*, start-

ing on the Puerto Rican bank, filled the northern islands. Somewhat fortuitously, the northernmost of the *roquet* group islands and the southernmost of the *bimaculatus* group islands were the last to be colonized by anoles. These islands were then filled up by moderate sized lizards of broad ecological adaptability, and the two groups were unable to establish themselves on islands already held. Figure 15 summarizes the biogeographic movements discussed.

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